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THE ECOLOGY AND ANATOMY OF POLYGONATUM COMMUTATUM.

BY RICHARD VOGT.

On account of its remarkably slow growth the plant which forms the subject of the following notes was expected to show peculiarities of both ecology and structure. The absence also of seedlings readily to be found by the superficial observer led us to seek more carefully for such specimens. As a result of these investigations we obtained what seemed to us rather interesting facts regarding the habits and the anatomy of the plant in various stages of development.

HISTORY.

The genus *Polygonatum*, to which the plant we have studied belongs, was first named by the Greek Dioscorides,[1] a contemporary of Pliny. The plants were recognized by the name *Polygonatum* by nearly all pre-Linnaean authors as will be seen in the accompanying list of synonyms. Some of the older authors using one worded names for genera took the common vernacular one corresponding to Solomon's Seal and called the plant *Sigillum Salamonis:* e. g., Brunfels, Gesner, and Tragus. Anguillara and Caesalpinus called the type plant of the genus *Frasinella.* Heister[2] rejected all older names and substituted the name *Salamonia* in honor of King Solomon. Linnaeus[3] did not recognize the genus of the ancients but referred the plants to his newly made genus *Convallaria* of which the lily-of-the-valley was the type. The plant on which Dioscorides founded the genus, and which since Linnaeus is still considered the type of the genus *Polygonatum*, is *Convallaria Polygonatum*, Linn. As early as 1549

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[1] Dioscorides, Mat. Med. 4 : 5.

[2] Heister, Syst. 5 (1748).

[3] Linnaeus, C., Sys. 1753); Gen. p. 96 (1737); p. 148 (1754); Sp. —Pl. p. 314 (1753).

Fig. 1

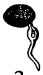
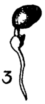


Fig. 2



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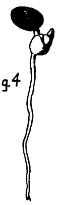

Fig. 4

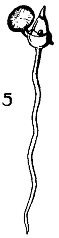

Fig. 5

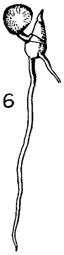

Fig. 6

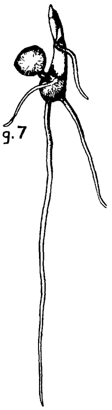

Fig. 7

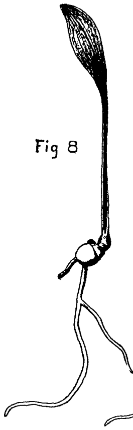

Fig 8

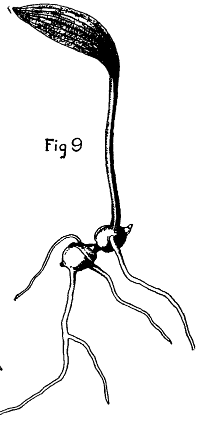

Fig 9

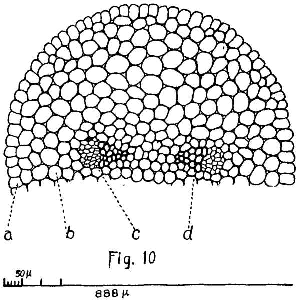

Fig. 10

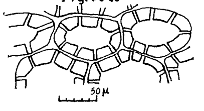

Fig. 10x

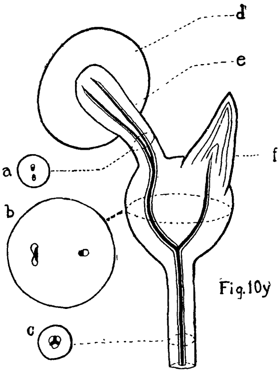

Fig. 10y

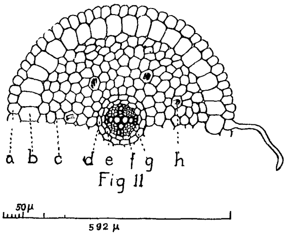

Fig 11

PLATE I. VOGT ON POLYGONATUM COMMUTATUM.

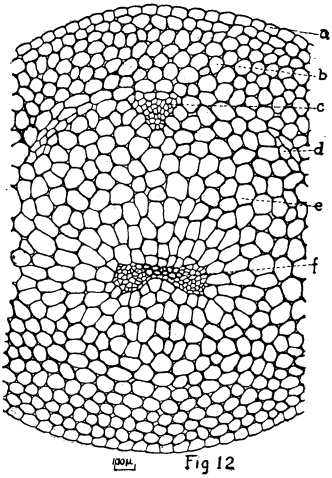

Fig 12

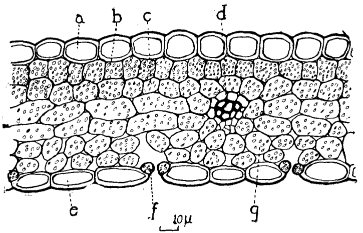

Fig 13

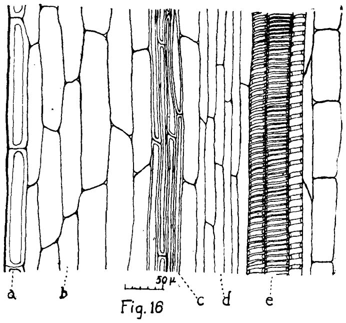

Fig. 16

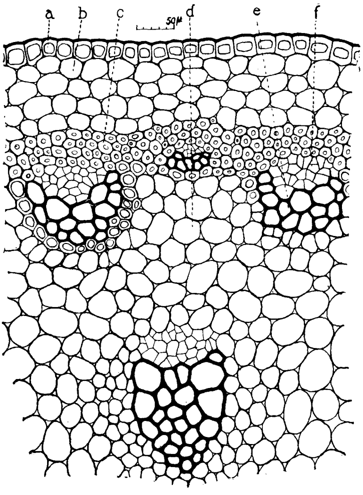

Fig. 17

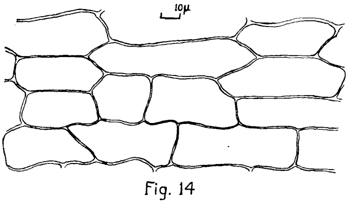

Fig. 14

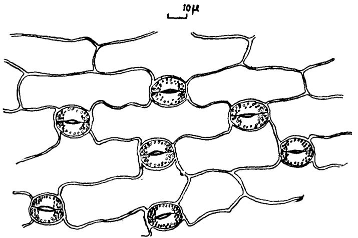

Fig 15

PLATE II. VOGT ON POLYGONATUM COMMUTATUM.

this plant had been called by Fuchs[4] by the correct and generally admitted binary name *Polygonatum latifolium.* As early as the fifteenth century and perhaps much earlier the plants were called Weiszwurz by the Germans, because of the characteristic white roots. All of the other contemporaneous European vernacular names were translations of the Latin *Sigilium Salamonis* or Soloman's Seal. Caspar Bauhin[5] explains the name as well as the Dioscorean one: "*quod radix crebro geniculata sit*" because the root is much geniculate "*Vulgo Sigillum Salamonis haud dubie a vestigiis pluribus radici sigilli instar impressis,*" "commonly Solomon's Seal doubtless because of the many (stem) traces impressed upon the root like a seal." Leonhard Fuchs[6] also had aptly accounted for the name nearly one hundred years before: "*Polygonatum Latinis dicitur. Officinis, item herbariis and vulgo Sigillum Salamonis, Germanis Weiszwurz* (*Gallis, signet de Salamo*) *hoc est radix alba nominatur. Polygonatum autem a radici geniculorum frequentibus nodis ex intervallis tumente appellaverunt.*" "(The plant) is called by the Latins *Polygonatum;* in the shops and by herbarians commonly Solomon's seal; by the Germans, Weiszwurz, that is, white root. *Polygonatum* they called it from the roots swelling at frequent intervals with bends and nodes."

In our region the genus is represented by two species *P. biflorum* Walt. Ell. and *P. commutatum* R. and S. The latter is the subject of this article. *P. commutatum* was first differentiated as a species from both European and other American members of the genus by Schulte under the name *Convallaria commutata.* Unaware of this publication Dietrich[8] had published this plant as new under the name *P. giganteum* by which it was known until recently in some of our common American manuals. Later he admitted the priority of P. *commutatum* as a specific name.[9]

The following is a resumé of the synomymy of the generic and specific names.

POLYGONATUM. Dioscorides, Mat. Med. 4:5.

Also *Polygonatum,* Matthioli, Lacuna, Castor Durante,

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[4] Fuchs, L., Primi de Stirpium Historia, p. 336 (1549).

[5] Bauhin, C., Pinax, p. 303 (1623).

[6] Fuchs, L. de Historia Stirpium, p. 199 b (1546).

[7] R. and S. Sept. 7., p. 1671 (1830).

[8] Otto and Dietr. Gartenz. 3 : 322 (1835).

[9] Otto and Dietr., Gartenz. 3 : 223 (1835).

Comerarius, Fuchs, Dodonaeus, Cordus, Gesner, Lobelius, Tabernaemontanus, Gerard, Lonicer, Cusa, Thalius, Clusius, Turner, Caesalpinus, and Bauhin. Tour., Els. p. 69 (1694); I. R. H., p. 78 (1700); Hill, Br. Herb. p. 320 (1756); Zinn., Cat, Pl. p. 59 (1760); Morandi, Hist. Bot. Pract. p. 105 (1761); Adanson, Fam. des Pl. p. 54 (1753). *Sigillum Salamonis.* Brunfels, Gesner, Tragus. *Convallaria.* Linn., Syst. (1735); Gen. p. 96 (1737), 148 (1754); Sp. Pl. p. 314 (1753) *Axillaria.* Raf., Jour. Phys. 89: p. 261 (1819). Am Month. Mag. 266, (1818).

Polygonatum commutatum. (R. and S.) Dietr., Gartenz. 3, p. 223 (1835).

P. giganteum l. c. p. 322. *Convallaria commutata* R. and S. Syst. 7, p. 1761 (1830).

ECOLOGY OF THE SEEDLING.

The young seedlings of the plant were found to be very common during the past summer at several places near South Bend, and an opportunity was thus afforded of studying them under natural conditions. They seem to thrive best in a well drained sandy soil with plenty of vegetable mold and in a position where they will be mulched and protected but not much shaded by surrounding trees.

The mature plant with its berries, after wilting or drying up, falls to the ground sometime in October, and the berries are soon covered with fallen leaves and other debris. In this state they soon rot leaving the seeds entirely embedded. The seeds themselves are somewhat roughly spherical in shape and about three millimeters in diameter; at first of a pale yellow collor with a brownish scar, they later become a dingy brown throughout. The bulk of the seed is found to be made up of endosperm food storage tissue of a horny consistency and composed of rather large cells, having thick and regular food deposits on the inner surface of their walls, and communicating with each other by numerous small canals (Fig. 10x). These seeds lie dormant during the fall and winter and germinate about the last of May or in early June, although they may sometimes be much retarded.

In germination the embryo breaks through the seed coat at a point about opposite the scar, and there are pushed out in succession; first the radical or primary root, next the hypocotyl which is soon slightly enlarged, and last the petiole of the cotyledon (Figs. 1 and 2.) (All drawings of the seedling are natural size.) The cotyledon itself remains inside the seed to act as an organ of absorption. The primary root now strikes downward into the soil and may attain a length of about five centimeters the first summer (Figs. 2 to 7.) Meanwhile the hypocotyl gradually increases in diameter, and a slit opens in its side through which the epicotyl or plumule first appears as a small conical bud (figs. 2 and 3). The epicotyl pushes out through this slit and grows to a length of about one centimeter during the first season, bearing usually two or three membranous leaf scales, and at its base one or two secondary roots (Figs. 4 to 7). In none of the many seedlings observed did the epicotyl produce a green leaf the first year, but in all cases the plant remained entirely underground until the second spring. It will be seen therefore that the plant, having no green leaves, can produce no new organic material but is dependant until the second summer on that stored in the seed. Such of this food material, however, as is not used in the first season's growth does not apparently remain in the seed, but is passed downward through the cotyledon and its petiole into the hypocotyl, where it is stored in a form probably far more readily available than the horny endosperm of the seed. This transfer is shown by the fact that before fall the seed and cotyledon are withered and soon afterwards decay, while at the same time the hypocotyl becomes enlarged, forming a tuberous body about the same in size as the original seed (Figs. 4 to 7). All, therefore, that the plant does during its first growing season is develop a root system, form a good-sized bud (the epicotyl), and transfer the remaining food from the seed into the hypocotyl where it will be ready for immediate use at the beginning of the second season. It will be seen that in this way the hypocotyl as well as the epicotyl takes part in forming the embryonic rhizome of the plant.

By the second spring the decay of the seed and cotyledon is complete, and the primary root now also withers away leaving thus two scars on the tuberous hypocotyl where these parts were once attached (Figs. 8 and 9). A single long-petioled green leaf is now sent up from the tip of the epicotyl; it will be noted that this is the first part which is visible above ground, the plant being in its second year of growth (Figs. 8, 9). During this second summer the old secondary roots also increase in size and new ones are sent out from various points on the epicotyl (fig. 9).

As fall approaches the epicotyl about the base of the leaf enlarges forming a second tuber similar in appearance to the old hypocotyl and separated from it by a narrow constriction (Fig. 9). In fall a rather large bud is produced in or near the axil of the leaf, and the leaf itself withers away, leaving an elongated scar on this second tuber. During the third summer a second single leaf and a third tuber are formed almost exactly like those of the previous year, and there is a further development of the root system. The leaf decays in fall leaving a long transverse scar on the third tuber.

The fourth year a true aërial stem with two or sometimes three leaves is sent up by most and probably by all of the seedlings not accidently retarded in growth. In no case was such a stem found earlier than the fourth year. In perfect plants then the fourth tuber is always found bearing a round stem scar produced by the dropping off of this first stem and readily distinguishable from the previous leaf scars. About this time, however, the first tuber or old hypocotyl usually decays, so that four-year-old rhizomes are not always found with four tubers. On this account it becomes increasingly difficult to determine the exact age of a plant by inspection only.

Moreover after the fourth year the constrictions between the tubers become less marked until in later life an almost continuous rhizome results with only joints and stem scars to mark the annual growth, the only decrease in diameter being in the parts formed at the time of seasonal droughts and fruit production in late summer and fall. There is a very gradual increase in the size of the successive aërial stems, and it is perhaps not until about the tenth year or even later that any flowers or fruit appear. Thus the development of the seedling is a very slow process, and, since the growth of the mature rhizome is by no means fast, it will be seen that some of the ordinary large branching colonies must be very old to have reached such a size.

THE ANATOMY OF THE SEEDLING.

GENERAL;NOTES ON THE VASCULAR SYSTEM (FIG. 10y DIAGRAMIC).

The primary root (c) has a single radical wood bundle, and this divides on entering the hypocotyl (b), one branch going upward into the petiole of the cotledon (a) and the other to the epicotyl (f) at the opposite side. That which enters the petiole of the cotyledon again divides and the branches continue almost to the end of the cotyledon where they gradually disappear. This bundle of the hypocotyl is seen about to divide in figure 12, f. The epicotyl (f) has at first no definite vascular bundles, but later a number of closed collateral bundles are formed most of which are in connection with the secondary roots that are sent out directly from the epicotyl. There is, however, some further development of conducting tissue leading from the hypocotyl into the epicotyl as lateral branches of the original bundle (Fig. 12,f). In the cross section of the hypocotyl (Fig. 12) the main bundle (c) with its branches (d) are seen in the form of a semicircle but as they approach the epicotyl they seem to take the form of an almost complete circle.

THE PRIMARY ROOT (FIG. 11).

The wood bundle of the primary root is of the radial type with alternating phloem (leptome) (f) and xylem (hadrome) (g) rays and is most often triarch but sometimes diarch or tetrarch as in the illustration. The xylem growth is exarch, and the ducts are of the ring and spiral types. The bundle is surrounded by a pericycle (e) of small flattened cells and an endodermis (d) which although not composed of thick walled cells is nevertheless very distinctive. The cortex (c) consists of about seven to ten irregular layers of short cylindrical parenchymatous cells which contain some raphides (h). The outer cortical layer is composed of larger cells (b), and these have a marked palisaded appearance. The epiblema cells (a) are small and rather thin walled even on the outer side.

THE HYPOCOTYL (FIG. 12).

The bundle (f) leading to the cotyledon shows in cross section as an irregular double row of xylem ducts with the phloem grouped about the ends of the row and on the side next the epidermis. The bundle (c) leading into the epicotyl is of the collateral type with what seems to be a nearly semicircular cambium strand (d) extending out a considerable distance on each side. This strand takes on the form of an almost perfect circle as it nears the epicotyl. In this semi-zone secondary bundles are later formed leading from the hypocotyl into the epicotyl. The space between these bundles is occupied by large cylindrical parenchyma cells (e), and the surrounding cortex (b) is of similar structure. The whole is enclosed by an epidermis (dermatogen) (a) with a slightly thickened outer wall.

THE COTYLEDON AND ITS PETIOLE (FIG. 10).

These have two wedge-shaped closed collateral bundles with xylem (d) directed inward and phloem (c) outward. These bundles are produced by the splitting of the single flattened bundle of the hypocotyl as shown in the diagram (Fig. 12). They are very well developed since all the water entering the seed and the entire food supply which is derived from it must pass through them. The remaining portions of the cotyledon are made up of simple parenchymatous tissue (b) with a thin walled epidermis (a).

THE EPICOTYL.

The epicotyl of a germinating seedling is made up of embryonic parts which have no marked vascular structure. Later its makeup is much the same as that of the mature rhizome into which it develops.

HISTOLOGY OF THE MATURE PLANT.

THE ROOT (FIG. 21).

The epiblema (a) of the root is composed of rather thin-walled cells somewhat elongated lengthwise of the root. Beneath these is a peculiar layer of enlarged cortical cells (b) having a palisaded appearance as in the primary root. The remainder of the cortex is made up of smaller cells (c), and in young roots is from eight to ten cell layers in thickness. Next in order are a well marked endodermis of thin walled cells (d), and a pericycle surrounding the central stele. The stele itself is of the radial type with from three to seven exarch xylem (hadrome) rays (g) and alternating phoelm (leptome) strands (f). Fig. 22 is a cross section of a heptarch or seven rayed bundle from a young root tip, showing the innermost layer of ordinary cortical cells (a), the endodermis (b), and the pericycle (c) before the cells have taken on their ordinary flattened appearance. Only the protoxylem (d) and protophloem (e) have been formed, the rest of the conducting tissue being as yet undeveloped. The large cells (f) embedded in the pith (g) form metaxylem a little later.

THE RHIZOME (FIGS. 18 and 19).

In the rhizome will be seen first the epidermis (Fig. 18,a, Fig. 19, a) of flattened brick-like cells with a thickened outer wall. Beneath these is the cortex (Fig. 18, b, Fig. 19, b) of roughly elliposoidal cells which gradually increase in size towards the center of the rhizome and merge without any line of demarcation into the large parenchymatous cells which make up the bulk of the organ. Many of these contain a few starch granules (Fig. 19, d), and there are a number of enlarged cells with raphides (Fig. 18, c, Fig. 19, c). The numerous scattered wood bundles vary in type from the closed collateral (Fig. 19, n) to those which are rather completely and typically amphivasal (Fig. 20). This transition shows the close relation that exists between these two types. The amphivasal bundles are mostly found in the center of the rhizome and in the older portion of its length, showing that they are a subsequent modification of the closed collateral. The xylem (Fig. 18, f, g, Fig. 19, e) is of the spiral and pitted types. The phloem (Fig. 18, h, Fig. 19, f) consists of the ordinary elongated sieve cells. Around each bundle there are one or two irregular layers of elongated cells which appear as a sheath (Fig. 18, d, e; Fig. 19, g), but these are not always distinctive. Fig. 20 shows an amphivasal bundle from the center of an old rhizome. The xylem (c) completely surrounds the phloem (f) and there are two sheath layers (a, b) separating the bundle from the surrounding parenchmatous tissue (e).

THE STEM (FIGS. 16. and 17).

The stem has an epidermis of brick-like cells with greatly thickened walls (Fig. 16,a; Fig. 17, a), Beneath this are found three or four layers of large thin-walled cortical cells (Fig. 16, b; Fig. 17, b). Next in order is a very distinctive zone of hardened schlerenchyma made up of cells whose walls are so much thickened that only a small lumen remains (Fig. 16, c; Fig 17, c). This schlerenchyma appears to develop from the cambium layer which earlier in the season formed the wood bundles. One small bundle (Fig. 17) is shown entirely embedded in the layer and most of those nearest it are at least partially surrounded. The remaining part of the stem enclosed in this schlerenchyma cylinder is composed of rather loosely arranged pith tissue (Fig. 17, d) which contains the numerous scattered vascular bundles. These are of the closed collateral type with the xylem (Fig. 16, e; Fig. 17, e) directed towards the center of the stem. The xylem consists mostly of spiral ducts, and the principle element of the phloem is the elongated sieve tube cells (Fig. 16, d; Fig. 17, f).

THE LEAF (FIG. 13, 14, 15).

The upper expidermis of the leaf (Fig. 13, a; Fig. 14) is composed of elongated and flattened cells with thickened walls. The lower epidermis (Fig. 13, l; Fig. 15) is simililar but is perforated by numerous stomata (Fig. 13, f). There are two palisaded cell layers immediately under the upper epidermis and these contain most of the chlorophyll (Fig. 13, b and c). Between the palisade cells and the lower epidermis the space is taken up by loose parencyhmatous tissue about four cells in thickness (Fig. 13, g). These cells have some chlorophyll and communicate with the stomata through the large intercellular spaces.

RESUME.

The following facts are considered to be peculiarly characteristic of the plant:—

1. No part of the seedling appears above ground the first year, but the plant simply transfers the food from the endosperm into its own storage parts and subsists upon it until the first leaf is completely developed during the second summer.
2. A single green leaf is sent up in the second year and another in the third year, but no aërial stem is produced before the fourth year.
3. When the fourth tuber of the rhizome has appeared, the first has usually rotted, making it difficult to estimate the age of a young plant by simple inspection.
4. A well marked vascular development of the cotyledon is a notable feature of the seedling anatomy.
5. In primary roots there is a variation of the plerome from diarch to tetarch and in secondary roots from triarch to heptarch.
6. Most of the wood bundles in the constricted portion of the annual growth are amphivasal while all of those in the thicker portion are collateral. What seems to be a probable explanation of this fact might be given here. The aërial stem is produced each year from a bud at the extremity of the rhizome, but the rhizome later continues growth beyond this point leaving the aërial stem in the position of a branch. The first part of this annual growth of the rhizome is a much thickened food storage organ, and since at this time it is not the in main line of water condition there is little use for xylem and the bundles there remain collateral. The continuations of these bundles in the later and more constricted

part of the annual growth are also at first collateral, but winter overtakes these in an undeveloped condition. The following spring most of these bundles divide at their growing point, part of the new elements going upward into a new aërial stem and part into a further extension of the rhizome. On account of the great demand for soil sap in the new stem the unfinished collateral bundles in the adjacent constricted part of last year's rhizome growth develop an unusual amount of xylem in connection with new secondary roots and become amphivasal. In the more distant expanded part of the rhizome the continuations of these bundles being already mature remain collateral as at first, but many of them develop excessive numbers of xylem elements which do not, however, encircle the phloem (Fig. 17.)

EXPLANATION OF THE FIGURES.

Figs. 1–9. Illustration of the stages of development of the seedling from the time of germination until the end of the second year's growth. All of the illustration are exactly life size. Fig. 1. Germinating seed with primary root and hypocotyl emerging. Fig. 2. Later stage with elongated primary root, swollen hypocotyl, and the slit through which the epicotyl is to emerge. Fig. 3. The epicotyl appearing through the slit. Fig. 4. Stage in the further development of the epicotyl and primary root. Figs. 5 and 6. Formation of secondary roots. Fig. 7. Elongation of epicotyl and production of leaf scales. Fig. 8. Seedling with leaf in second season of growth. The cotyledon has disappeared and the primary root is withering. Fig. 9. A later stage in the second year's growth showing the formation of the second tuber.

Fig. 10. Cross section of the petiole of the seedling cotyledon. (a) epidermis, (b) cortical tissue, (c) phloem, (d) xylem.

Fig. 10x. Food storage cells of the seed endosperm.

Fig. 10y. Longitudinal diagrammatic section of the tissue systems in a young seedling. The side figures show diagrammatic cross sections at the places indicated by the dotted lines. (a) petiole of cotyledon, (b) hypocotyl, (c) primary root, (d) seed, (e) cotyledon, (b) epicotyl.

Fig. 11. Cross section of the primary root of the seedling. (a) epiblema, (b) palisaded layer of the periblem, (c) ordinary periblem cells, (d) endodermis, (e) pericycle, (f) phloem and (g) xylem, constituting the plerome, (h) raphides.

Fig. 12. Cross section of the hypocotyl. (a) dermatogen, (b) periblem, (c) bundle leading to epicotyl, (d) cambium layer, (e) central parenchymatous tissue, (f) bundle leading to cotyledon.

Fig. 13. Cross section of the leaf of amature plant. (a) upper epidermis, (b and c) palisaded layer, (d) wood bunble, (e) lower epidermis, (f) stoma, (g) loose chlorenchyma.

Fig. 14. Surface view of upper epidermis showing cell structure.

Fig. 15. Surface view of lower epidermis containing stomata.

Fig. 16. Longitudinal section of mature stem taken late in season when growth in thickness had ceased and all of the tissues were in permanent condition. (a) epidermis, (b) cortex, (c) schlerenchyma, (d) pith, (e) xylem, (f) phyloem.

Fig. 17. Cross section of the same. (a) epidermis, (b) cortex, (c) schlerenchyma, (d) pith, (e) xylem, (f) phloem.

Fig. 18. Longitudianl section of mature rhizome. (a) epidermis, (b) cortex, (c) cell containing raphides, (d and e) sheaths of elongated cortical cells, (f and g) xylem, (h) phloem. The bundle is amphivasal, and a duct is shown at the extreme right.

Fig. 19. Cross section through the mature rhizome. (a) epidermis, (b) cortex, (c) cell with raphides, (d) starch granules, (e) xylem, (f) phloem in an almost amphivasal bundle, (g) sheath of cortical cells, (h) a small typical collateral bundle.

Fig. 20. Cross section in detail through a more typical amphivasal bundle from center of an old rhizome. (a and b) sheath layers, (c) xylem, (d) cells which will later from xylem, (e) cortex, (f) phloem.

Fig. 21. Cross section of a small secondary root. (a) epelbema, (b) outer palisaded layer of periblem, (c) ordinary periblem cells, (d) endodermis, (e) pericycle, (f) phloem, (g) xylem.

Fig. 22. Cross section of the wood bundle from the tip of a larger seconadry root on an older part of the plant. (a) periblem, (b) endodermis, (c) periclycle, (d) xylem, (e) phloem, (f) cells which form meta-xylem, (g) pith cells.

The scale of magnification accompanies each figure.

ABNORMAL FLOWERING OF HEPATICA.

BY J. A. NIEUWLAND.

The tendency to redundancy of sepals in Hepatica, our common liver-leaf, a plant that adds so much to the beauty of our early spring woods, was noticed several hundred years ago by Lobelius[1] or as he is also known de l'Obel. He even gave the double flowered plant the varietal name, customary in those days, calling it *Hepatica trifolia polyanthos*, or doubled flowered *Hepatica trifolia*. Parkinson[2] in 1629 also describes such plants under practically the same name. The Liverleaf itself was even earlier called Hepatica by Bock[3] in Brunfels great work of botany, the first that included good natural lifelike illustrations of plants in the sixteenth century.

Since in this plant it may be considered that the so-called "sepals" arise by the change of the stamens into these in doubling,

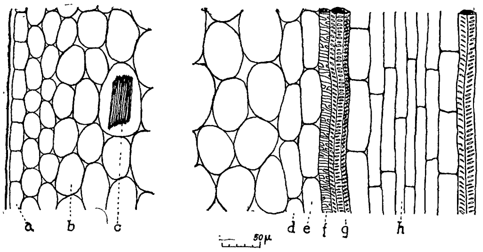

Fig. 18

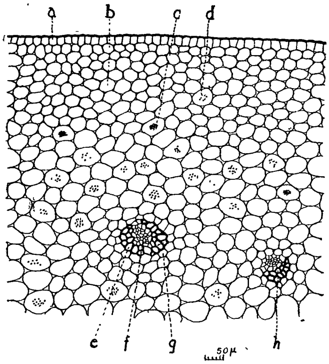

Fig. 19

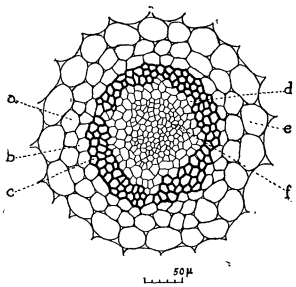

Fig. 20

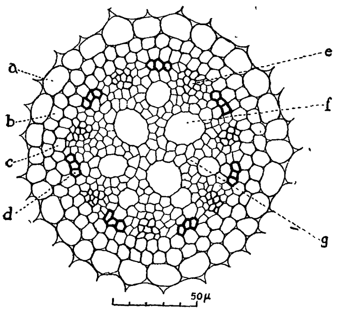

Fig 22

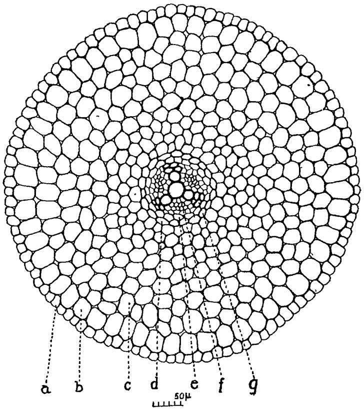

Fig. 21

PLATE III. VOGT on POLYGONATUM COMMUTATUM.